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ON THE ECOLOGY OF *ALEURODES BRASSICAE* WALK. (HEMIPTERA)

By C. G. Butler, M.A., Ph.D.

(*The Entomological Department, Zoological Laboratory, Cambridge.*)

With Five Text-Figures.

[Read 1st June, 1938.]

Communicated by Dr. A. D. Imms, F.R.S., F.R.E.S.

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1. Introduction.

The present investigation has particular reference to the relationship between the whitefly *Aleurodes brassicae* Walk. and the biotic and physical characters of its environment. It was carried out at the Entomological Field Station and the Zoological Laboratory, Cambridge University, during the tenure of a scholarship from the Ministry of Agriculture and Fisheries. All the whiteflies used in these experiments were derived from specimens collected in a garden in Cambridge during 1935, unless a definite statement in the text is made to the contrary. I am deeply grateful to Dr. A. D. Imms, F.R.S., for his advice and criticism, and to him and to Professor J. Stanley Gardiner, F.R.S., for their constant encouragement.

2. Description of the developmental stages.

It was considered necessary to describe the larval instars of *A. brassicae*, since Deshpande (1933) does not figure them in sufficient detail to be clearly distinguished from one another, and Weber (1935) only described the structure of the adult insect.

Egg (fig. 1).

Elongate, pyriform, with a small pedicel attached at the broader end. Length, without pedicel, about 0·26 mm. Length of pedicel about 0·032 mm. Width of egg at widest part

just over ½ length. When freshly laid the egg is covered with a white meal-like wax, if this is removed the egg is seen to be a pale shining yellow. The colour changes to brown and

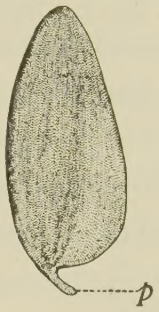

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Fig. 1.—Egg of *A. brassicae*. × 141·5. *p* = pedicel.

later to dark brown before hatching, eclosion takes place by means of a slit at the narrower end through which the larva crawls.

Larva, 1st instar.

On emergence the larva is pale creamy white, but soon becomes pale yellow. It is approximately 0·34 mm. long and the greatest width is about ⅔ of the length. Shape oval, slightly convex dorsally, flattened ventrally. On the minutely crenulate margin sixteen pairs of small bristles arise, of which the two posterior pairs are prominent and long. The abdominal, but not the thoracic, segments are clearly demarcated. A few hours after

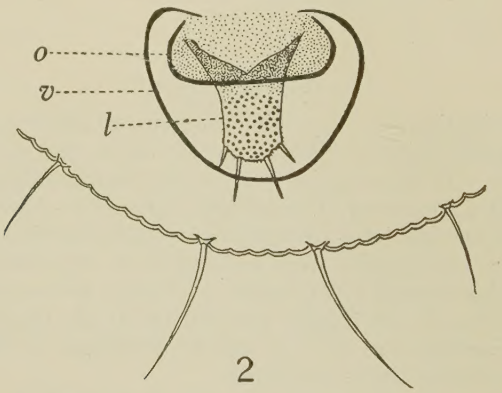

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Fig. 2.—Dorsal view of vasiform orifice of 1st instar larva. × 294.
l = ligula; *o* = operculum; *v* = vasiform orifice.

emergence the larva becomes covered with a white meal-like wax, which collects particularly on the marginal bristles. Three pairs of functional five-segmented legs are present and a pair of three-segmented antennae, about ⅓ of the length of the body. The vasiform orifice is relatively large compared with later instars, and is subcircular in shape. Operculum flap-like; the ligula covered with short hairs with one pair of long bristles and one pair of short bristles at its apex (fig. 2). The larva appears to remain active for about three days after emergence from the egg, after which time it settles down and becomes attached to the leaf surface by its mouthparts.

Larva, 2nd instar.

About 0·56 mm. long, width about $\frac{3}{5}$ of the length. Roughly oval in shape, with broad white marginal fringes of wax. Translucent yellow in colour directly after moulting, but this turns a little brownish after a few days. Dorsum smooth. Segmentation not yet defined in the thorax but clearly evident in the abdomen. Legs non-functional and vestigial, antennae atrophied. Marginal hairs lost except for two prominent pairs on the posterior end of the body and one anterior pair. Vasiform orifice subcordate, operculum flap-like; ligula spatulate covered with small hairs, and possessing one pair of prominent bristles at its apex (fig. 3).

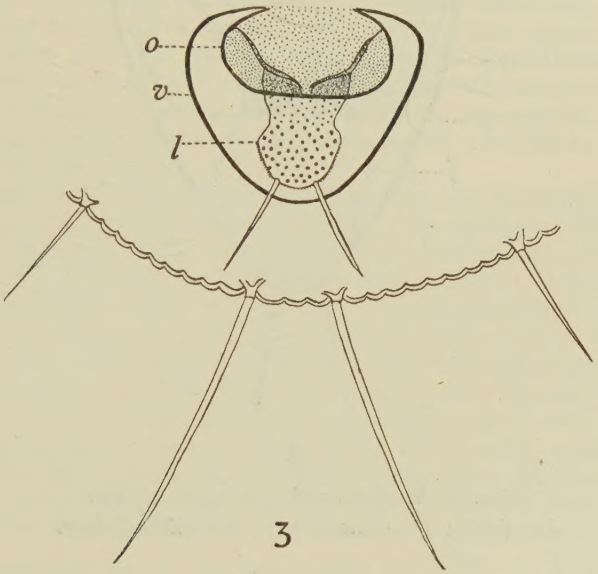

FIG. 3.—Vasiform orifice of 2nd instar larva. × 294.
l = ligula; *o* = operculum; *v* = vasiform orifice.

Larva, 3rd instar.

About 0·76 mm. long, width about $\frac{5}{7}$ of the length. Roughly oval in shape, but in older specimens dorsum slightly more humped than in previous instars; usually with broad white marginal fringes of wax. Translucent yellow in colour directly after moulting, often changing to a brownish shade in older specimens. Dorsum smooth. Thoracic segments cannot yet be distinguished with certainty, but the abdominal ones are clear. Legs and antennae non-functional and greatly atrophied. No hairs on crenulate margin, except for one pair of stout bristles at posterior end of the body. Vasiform orifice subcordate but longer than in previous instars, operculum flap-like; ligula spoon-shaped but convex, covered with small hairs and possessing one pair of prominent bristles at its apex.

Larva, 4th instar or pupa.

About 1·51 mm. long, width about $\frac{2}{3}$ of the length. Roughly oval in shape, but dorsum usually markedly humped, often with broad white fringes of wax. Yellow or brown in colour at first, but some specimens translucent yellow. In the latter the adult can be seen developing. Red eye-spots of adult clearly seen in most specimens. Colour often changes to dark brown shortly before emergence of adult which occurs by means of a dorsal longitudinal slit with a V-shaped slit at its anterior end. Sex of adult very obvious

at this stage as eggs of female may be seen clearly. Shortly before emergence of adult, pupa becomes covered with a dirty-white meal-like wax. Thoracic as well as abdominal segments distinct. Pupa adhering to leaf surface by wax only. Legs and antennae non-functional and greatly atrophied. No hairs on crenulate margin, except for one pair of long stout bristles at posterior end of body. Vasiform orifice (fig. 4) as in third instar.

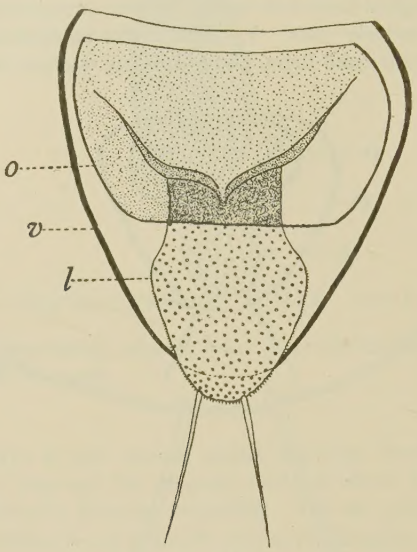

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Fig. 4.—Vasiform orifice of pupa. × 294.
l = ligula; *o* = operculum; *v* = vasiform orifice.

3. The annual cycle.

The number of generations of *A. brassicae* produced per annum apparently varies from year to year. During 1935 five complete generations occurred in the field in Cambridgeshire, whereas in 1936 only four generations were completed in most localities; but, in some of the more sheltered places in Cambridgeshire, a fifth generation occurred, being the progeny of those individuals of the fourth generation that had emerged earliest. It should be mentioned that the generations overlap to a considerable extent, and this makes it very difficult to determine the precise number of generations in any one year.

Immediately adult *A. brassicae* reach a suitable host-plant, they always begin to move towards the undersurface of the leaves, and, by the end of two hours, 95% of those liberated are found in this position. This phenomenon occurs in nature as well as in the laboratory, and *A. brassicae* is always found in this position. Having reached the undersurface of the leaves of the host-plant the adults start to conduct their normal life. Since their reactions differ according to the general atmospheric temperature and other factors, it will be best to consider them under: (*a*) Summer conditions with relatively high temperature; (*b*) Winter conditions with relatively low temperature.

(a) *Under summer conditions*, which extend from about the middle of May until the end of September, the mean daily temperature is generally near the optimum for *A. brassicae* and consequently their activity is at its height.

Having reached the undersurface of the leaf the adult whiteflies spread out fairly evenly over it and immediately insert their stylets into the plant's tissues. Unless the plant dies, or the whiteflies are disturbed in some way, they will remain with their stylets inserted for the rest of their lives, except during the rare and short periods when they move to new positions on the leaf surface.

The male whiteflies, still with their stylets inserted, pair with one of the nearest females. Pairing takes place in a lateral position, and a male will pair with the same or other females on several occasions. Each coition may last for some hours. About ten days after its first pairing the male insect dies, but if it is prevented from pairing it may live for several weeks.

Both sexes have large abdominal wax glands which appear to secrete wax the whole time, and with this the insect forms its characteristic circular wax patch by walking round in a circle using its inserted proboscis like the fixed point of a pair of compasses. So far as can be determined, by taking the melting-point by micro-methods, the wax secreted is similar to that of the leaf surface of the host-plant.

The female insect deposits her eggs in a circle near the periphery of the wax patch which she has produced, moving round a short distance after each egg has been laid. The eggs which have already been laid become covered with wax by contact with the female's body as she moves round. Oviposition so far as can be detected takes place only by day. Having completed one " egg-ring," the female moves to a new position on the leaf surface to form another. Each female whitefly, under optimal conditions, apparently lays about 20–100 eggs, copulation commencing even before the wings become dry and pigmented after emergence. Two or three days later oviposition commences and continues spasmodically until the natural death of the female some months later. The eggs hatch in about a week and the adults emerge from the pupae three or four weeks later, the males tending to emerge slightly before the females. The sex ratio, as determined from 3,000 individuals collected in the field as pupae in June and hatched out in the laboratory, is $\frac{\text{males}}{\text{females}} = \frac{12}{12{\cdot}1}$, slightly more females than males being produced.

On emergence the adults move to an unoccupied portion of the leaf upon which they were reared. If, as is usually the case, the leaf shows signs of wilting or overcrowding, they move to the next highest leaf of the host-plant or migrate to a fresh plant and there begin their adult life.

(b) *Under winter conditions*, which extend from the end of September until the middle of May, the mean daily temperature is below the optimum for real activity of the whitefly.

It was found in the field that, after some frost, from October onwards, the adult whiteflies were becoming much less numerous on broccoli, sprouts, kale, etc., than they had been during the previous months. This falling off in numbers is well shown in table 1 below.

It will be noticed from table 1 that while the number of adults on broccoli, sprouts and kale decreased during the period September to January, the number on savoy cabbage increased very considerably. From this it would appear that adult whiteflies were actually migrating from the broccoli, etc., to the savoy plants as the cold weather increased. That this migration was for the purpose of obtaining the much greater shelter afforded by the crevices on the underside of the savoy leaves, in comparison with the shelter afforded by the other host-plants present in the field at this time of year, seems fairly obvious. This is supported by the fact that, at the time of the first count and, at all ten

previous counts, starting in June when the infestation was very heavy, the savoys were by far the most lightly attacked, even though they were planted at the same time as the other cabbage varieties and in between them. It would thus appear that savoys, although not a favourite summer host, are a favourite winter one.

TABLE 1.

Date	Broccoli	Sprouts	Kale	Savoy	Sex ratio
11.ix.1935	111·4	299·2	122·8	39·6	$\frac{1}{1{\cdot}03} = \frac{♂♂}{♀♀}$
25.x.1935	31·4	172·6	50·4	74·2	$\frac{1}{3{\cdot}11} = \frac{♂♂}{♀♀}$
1.xi.1935	16·4	58·0	12·6	101·6	$\frac{1}{5{\cdot}54} = \frac{♂♂}{♀♀}$
7.xi.1935	16·2	47·4	10·2	304·4	$\frac{1}{6{\cdot}93} = \frac{♂♂}{♀♀}$
17.xii.1935	15·4	40·8	3·4	322·0	$\frac{1}{36{\cdot}6} = \frac{♂♂}{♀♀}$
6.i.1936	8·0	11·2	2·4	1109·4	All ♀♀

The average number of adult whitefly per plant, found on four cultivated varieties of *Brassica oleracea* during the winter 1935–1936. The averages were calculated from counts made on five plants of each kind picked out at random from a large plot at each time of counting. The sex of the specimens collected was also determined and the ratio of males to females, as determined from all the specimens collected, is given in the last column for each time of counting.

It was noted in the field that, as the average daily temperature decreased, adult whiteflies tended to congregate together in the more sheltered parts of the plant. Thus the axils of the leaves and the furrows on either side of the mid-rib of the leaves of broccoli and sprouts became crowded with whitefly, and by January it seemed impossible that these places could harbour any more.

Throughout the autumn and early winter months, on warm days when the humidity was high, large numbers of whiteflies could be seen migrating, and counts made at the time showed that they were often moving to the savoy plants.

It will also be noticed from table 1 that the numbers of males in the field fell off from approximately 50% of the adults present in September and during the summer months, to 0% by the beginning of January. Thus it appears that the males are far less tolerant of cold than the females. To a large extent laboratory experiments support this view, since it was found that females can withstand a temperature as low as −18° C. for twelve hours at a time with only a 12% mortality, at the beginning of October, whereas only 30% of the males could withstand this treatment. The above experiment was carried out on a large scale, some 500 individuals of each sex being used. These individuals were collected at random in the field immediately before each experiment, placed on a freshly cut cabbage leaf in a lamp-glass, the ends of which were covered with muslin, the whole being placed in a refrigerator at room

temperature. The temperature was then slowly lowered until the lowest temperature required had been reached, and it was maintained at this level for twelve hours, at the end of which time the process was reversed until room temperature was reached once again. The number of whiteflies living was ascertained some two hours later, as was that of the control experiment which had been running at a temperature of 25° C. during the same period. Never more than 2% of the controls died during this period, so that the experiments may be regarded as significant.

In later experiments it was found that males that had no opportunity to copulate could withstand as low a temperature as the females, about 87% surviving, whereas males that had been observed in copulation died at a temperature no lower than —4° C. It was also found that at room temperature those males that had no opportunity for copulation lived for about three weeks, whereas males that had copulated only lived for about a week after the first coitus.

TABLE 2.

Date	No. of eggs	No. of 1st instar larvae	No. of 2nd instar larvae	No. of 3rd instar larvae	No. of pupae	Plant
11.ix.1935	11·2	22·8	8·6	4·8	39·8	Broccoli
	92·2	55·8	22·6	5·8	1·2	Sprouts
	63·4	4·8	2·4	0·8	8·8	Kale
	9·4	3·4	0·6	0·0	0·0	Savoy
25.x.1935	6·0	3·4	5·4	4·0	36·2	Broccoli
	56·4	13·8	4·4	15·8	61·8	Sprouts
	12·8	10·8	6·0	15·4	31·4	Kale
	6·0	10·0	3·8	1·4	6·4	Savoy
1.xi.1935	2·8	0·8	0·8	2·0	0·8	Broccoli
	9·8	2·8	1·6	1·8	3·4	Sprouts
	0·8	1·6	0·8	1·8	0·8	Kale
	14·2	3·6	0·8	4·0	2·0	Savoy
17.xii.1935	0·8	0·2	0·0	0·0	0·0	Broccoli
	1·2	0·2	0·0	0·0	0·0	Sprouts
	0·2	0·0	0·0	0·0	0·0	Kale
	4·8	0·4	0·0	0·0	0·0	Savoy
6.i.1936	0·0	0·0	0·0	0·0	0·0	Broccoli
	0·2	0·0	0·0	0·0	0·0	Sprouts
	0·0	0·0	0·0	0·0	0·0	Kale
	5·4	0·0	0·0	0·0	0·0	Savoy

The average number of eggs and larvae of *A. brassicae* found on four varieties of *Brassica oleracea* during the winter 1935–1936. The averages were calculated from counts made on five plants of each kind picked out at random from a large plot each time a count was made. After each count five fresh plants of each variety were chosen for the next count, and all the eggs and young stages were carefully removed from them with as little disturbance as possible to the adults present.

Females brought into the laboratory at any time during the autumn or winter, and placed under suitable conditions, always began to oviposit in the normal manner within the first week and usually within the first three days. Likewise, if a female was dissected, eggs, apparently fully mature, were always

found. It therefore appears that the female *A. brassicae* are fully mature throughout the winter, but, unlike the males, cold does not kill them but merely arrests oviposition.

A further proof that the males were dying off under the influence of cold in the field during the early winter, was obtained by placing rings of black paper covered with " sticky-foot " beneath different varieties of *Brassica oleracea*. It was then found that of 204 specimens that had dropped on to the paper and adhered to the " sticky-foot " during the course of a week, only seven were females. It was also noted that the number of individuals collected in this way was always greatest after a severe frost.

Later in the season it was found, in the laboratory, that the females were far less tolerant of severe cold than they had been previously. In an experiment conducted on 20th March, 1936, on females that had left the overwintering clusters on the advent of warmer weather, 500 females were subjected to a temperature of —14° C. and only 27% survived. At this time large numbers of females were found adhering to the " sticky-foot " discs after two nights of frost and it was known that they had not oviposited to any extent.

With regard to the other life-history stages of *A. brassicae* throughout the autumn and winter, it was found that, as the mean daily temperature fell as the season progressed, so the rate of oviposition of *A. brassicae* decreased, until by November, little or no oviposition was occurring. This is clearly seen in table 2, which gives the results of counts of the various life-history stages, other than adults, on four varieties of *Brassica oleracea* throughout the winter.

4. Parthenogenesis and the sex ratio.

Experiments with females, isolated in the pupal stage, have shown that there is a great tendency for unfertilised eggs to produce males. Fertilised eggs, on the other hand, produce approximately equal numbers of males and females. Fifty experiments, in each of which ten females were used, were conducted at 18° C. and 80% relative humidity, to study this point. The results, which are typical, obtained from two of these experiments, are given in tables 3 and 4.

Table 3.

♀	Total no. of eggs	No. of pupae produced	No. of dead pupae	Ratio of ♂♂ to ♀♀
1	78	69	2	1 : 1·03
2	64	52	2	1 : 1·00
3	36	31	0	1 : 1·07
4	37	31	1	1 : 1·14
5	48	36	1	1 : 1·19
6	51	45	1	1 : 0·96
7	93	83	0	1 : 1·02
8	24	21	1	1 : 1·00
9	82	72	2	1 : 1·06
10	71	58	1	1 : 1·03
Total	584	498	11	Mean 1 : 1·05

The results of an experiment to determine the sex ratio of individuals from fertilised eggs.

TABLE 4.

♀.	Total no. of eggs	No. of pupae produced	No. of dead pupae	Ratio of ♂♂ to ♀♀.
1	72	61	1	1 : 0·07
2	50	44	3	1 : 0·28
3	55	48	0	1 : 0·20
4	45	40	0	All ♂♂
5	42	32	0	1 : 0·06
6	18	15	0	All ♂♂
7	49	42	2	1 : 0·08
8	67	56	6	1 : 0·31
9	90	78	3	1 : 0·23
10	33	26	2	All ♂♂
Total	521	442	17	Mean 1 : 0·12

The results of an experiment to determine the sex ratio of individuals from parthenogenetic eggs.

The sex ratio as calculated from the results obtained in all of the experiments was $\frac{1}{1{\cdot}04} = \frac{♂♂}{♀♀}$ for fertilised eggs, and $\frac{1}{0{\cdot}09} = \frac{♂♂}{♀♀}$ for parthenogenetic eggs.

As may be seen from these results, there tends to be a slightly higher rate of larval mortality in the case of those individuals produced from parthenogenetic eggs. Since the unfertilised eggs largely produce males it may be argued that the male larva is less hardy than the female, and this may account for the fact that slightly more females than males are always to be found in the field throughout the summer months.

It is of interest to compare these results obtained with *A. brassicae* with those of other workers on ALEYRODIDAE.

Morril and Back (1911) showed that in the Citrus whitefly, *Aleurodes citri* Riley and How., parthenogenetic eggs give rise to males only. The most complete work, however, seems to have been done on the greenhouse whitefly, *Trialeurodes vaporariorum* Westw. Morril (1903) reported that in America the unfertilised eggs of this species always give rise to males. This observation was subsequently confirmed by Schrader (1920). On the other hand the breeding experiments of Hargreaves (1915) and Williams (1917) showed that in England unfertilised eggs of this species nearly all give rise to females. It therefore appeared that there were two biological races, one in America and the other in England, which differed in their reproductive processes. In 1922, however, Lloyd (1922) obtained results which indicated that in the Lea Valley the reproductive behaviour of *T. vaporariorum* was like that of the American race, and Schrader (1926) showed that generally throughout England there was no longer the vast preponderance of females noted by Hargreaves (1915) and Williams (1917), and he was unable to obtain stocks in which virgin females gave rise to a preponderance of females.

Schrader (1926), working on material sent to him by Williams in 1920, was able to give cytological evidence which tended to show that only two classes of individuals were present in the English race (as described by Williams (1917)), just as in the American race, that is, females with 22 chromosomes and males with 11 chromosomes; but he was unable to settle the question of the origin of the few males that occur in the English race.

Thomsen (1927) has shown that the English and American races of *Trialeurodes vaporariorum* will pair with one another, the offspring being all females which in turn produce females from unfertilised eggs. The eggs of the female-producing, or English, strain have a typical maturation process with two maturation divisions in which the chromosome number is reduced from 22 to 11. It is just possible that there is some difference in meiosis between the English and American races. After the second maturation division the diploid state in unfertilised female-producing eggs is restored by some type of auto-regulation, and Thomsen suggests that this is brought about by the splitting of the chromosomes, as no nuclear division follows.

In the case of *Aleurodes proletella* L., Thomsen (1927) found that unfertilised eggs are male producing, and fertilised eggs give rise to females. He also showed that impregnated females can lay both fertilised and unfertilised eggs. All the eggs produce two polar bodies by which the chromosome number is reduced to the haploid condition. Unfertilised eggs remain haploid, whereas fertilised eggs become diploid again, the males therefore being haploid and the females diploid.

Thomsen showed that during spermatogenesis a synapsis fails, although the spermatocytes have a definite growth period. There ensues only a division without any further reduction in the number of chromosomes present; the spermatozoa are therefore haploid.

The conditions described by Thomsen (1927) as occurring in *Aleurodes proletella* would seem to be the one most nearly akin to that of *A. brassicae*, and it is possible that this species has a similar cytological history. It should, however, be pointed out that no explanation has been put forward to account for the presence of the few males that occur in the English, *i.e.* female-producing, race of *Trialeurodes vaporariorum*, and the origin of the few females derived from unfertilised eggs in *Aleurodes brassicae* is similarly quite unexplained.

(5) Host selection.

If a reasonably complete study of the relationship between *A. brassicae* and its environment is to be made, it is of great importance to discover on what cultivated and wild plants the whitefly can live, and upon which it can breed. As a preliminary it is necessary to find out exactly how long the adult whitefly can live with, and without, food at some definite temperature and humidity. For these experiments, which were conducted on a large scale, a glasshouse at the Entomological Field Station was chosen with a controlled temperature varying from about 18° C. to 20° C. throughout the twenty-four hours. Approximately 95% relative humidity was maintained by means of cellophane cages placed over the growing plants on which the experimental insects were kept, and the continual loss of water by the plant during transpiration and from the soil preserved this high humidity within 3% throughout the whole experiment.

The experiments were conducted during June and July 1936 when the sunlight was sufficient for good plant growth, and the whiteflies were breeding most actively in the field. In every case 200 newly emerged and mated females were used and a control experiment run at the same time. It was found that the average length of life of an adult female whitefly kept under these conditions on young cabbage plants (Sutton's "Enfield Market" variety) was about thirty days, but females kept under identical conditions of temperature and humidity without any food plant lived, on an average, from 2·5 to 4 days.

These preliminary observations led to the adoption of a twelve-day period of life on any given plant under these conditions of temperature and humidity as an indication that adult female *A. brassicae* could live on it, but successful oviposition and rearing of progeny was taken as a more definite indication of the ability to live on a plant. In this way it was found that *A. brassicae* could live and breed upon the following varieties of *Brassica oleracea* : spring cabbage, summer cabbage, purple sprouting broccoli, white sprouting broccoli, broccoli, cauliflower, kohl rabi; also on *Cheiranthus* sp., *Taraxacum dens-leonis*, and *Sonchus oleraceus*; and that it could not live and breed on the following plants : *Brassica oleracea* variety pickling cabbage, *Raphanus sativus*, *Brassica rapa*, *Brassica rapa* variety swede turnip, *Brassica campestris*, *Sisymbrium officinale*, *Capsella bursapastoris*, *Aubrietia* sp., *Mathiola* sp., *Coleus* sp., *Myosotis alpestris*, *Cucumis pubescens*, *Solanum tuberosum*.

The above list contains Cruciferae and other plants on which *A. brassicae* adults have been seen in the field, and it was necessary to find out whether they could act as hosts to the insect. It does not claim to be a complete list of the host-plants of *A. brassicae*, but contains most of the commoner ones found in the field.

Adult females alone were used for the experiments, as the length of life of the male seems to be directly connected with the amount of copulation which it undertakes. There is, however, every reason to believe from other observations that it can live on the same host-plants as the female.

The question whether *A. brassicae* shows any preference for one host-plant over another has been examined in some detail both in the laboratory and in the field. In the laboratory, experiments were undertaken to discover whether there was any order of host preference of *A. brassicae* for ten cultivated varieties of *Brassica oleracea*, together with dandelion (*Taraxacum*) and sowthistle (*Sonchus*). For this purpose a single specimen of each of the twelve varieties of plants was placed in each of twelve large cellophane cages. The humidity in the cages varied about 4% from 96% relative humidity, and the temperature varied from 18° C. to 20° C. throughout the experiment. At the top of each cage 1000 newly emerged adult females and an equal number of newly emerged adult males were liberated and allowed to distribute themselves in a random manner. At the end of a month counts were made of the number of third instar and pupal stages present on each plant. The results arranged in order of host preference are given in table 5.

The surface area of the leaves of the plants from the laboratory and field experiments were found by means of the formula of Meeh (1879) $\frac{(\text{Area})^3}{(\text{Weight})^2} = k$, based on the law that the surfaces of similar solids are proportional to the two-thirds power of the volume, assuming that the specific gravity is constant. To apply this formula the constant k must first be calculated for each kind of plant as it varies with each species (Simanton 1933). This was obtained by measuring the actual surface area of 100 leaves from each kind of plant by drawing their outlines when they were pressed flat upon paper, and using a planimeter to measure the area enclosed. In every case the wet weights were taken within half an hour of cutting. Having obtained the constant for each kind of plant, the surface area of the undersurface of each leaf examined could readily be calculated from its wet weight. Only the undersurface of the leaf was considered, since it is on this surface that the larvae and pupae are found. The error of the calculation of surface area by this method was found to be never more than 1%.

Table 5.

Plant	Maximum no. of larvae per square inch of leaf surface	Mean no. of larvae per square inch of leaf surface	Minimum no. of larvae per square inch of leaf surface
" Extra Curled " scotch kale	6·42	3·14	1·90
Sowthistle	5·31	2·43	1·21
" Standwell " broccoli	5·22	2·19	1·06
" Magnum Bonum " cauliflower	4·98	2·03	1·01
" Wroxton " brussels sprouts	4·76	1·93	0·95
Purple sprouting broccoli	2·62	1·30	0·60
" Perfection " broccoli	2·15	1·11	0·57
White sprouting broccoli	1·09	0·61	0·30
Spring cabbage	0·77	0·35	0·16
Dandelion	0·51	0·23	0·10
" Enfield Market " cabbage	0·09	0·04	0·01
" Best of All " savoy	0·06	0·02	0·00

Ten cultivated varieties of *Brassica oleracea*, together with dandelion and sowthistle, arranged in the order in which they were chosen as hosts by *A. brassicae* in laboratory experiments.

All varieties were obtained from Messrs. Sutton and Sons, Reading.

A large-scale field experiment was undertaken to give natural confirmation to the results obtained in the laboratory. The plants, in the field experiment, were grown in plots, each plot being nine feet square and containing nine plants of the same variety. The plots were arranged on the latin square system, so that the same combination of plants never occurred twice. Although it has been argued that the latin-square system does not give a truly random distribution, it seems to be the best experimental method so far evolved for getting such a distribution of the plants.

Control was undertaken of the Cabbage Root Fly, *Hylemyia brassicae*, by watering each plant, thrice at ten-day intervals after planting out, with a solution of corrosive sublimate (one ounce to ten gallons of water), each plant receiving about $\frac{1}{4}$ of a pint at each application. Various species of flea beetles, *Phyllotreta* sp., were also controlled by dusting, when necessary, with derris powder.

The plants became infected with *A. brassicae* quite naturally, probably from the surrounding gardens and land. Quite a high degree of natural infection was obtained. At the beginning of September counts were made of the number of third instar and pupal stages present on the different varieties. September was chosen as the most convenient time of year for making counts as the drop in temperature of the atmosphere retards development, and during the period of counting very few whiteflies emerged from the pupae.

As most of the whiteflies at this time of year are in the adult, third instar, or pupal stages (the adults being individuals that emerged late from the pupae of the previous generation) the counting was greatly facilitated, the number of first and second instar individuals being so small that it could be neglected. Also, by September, the whiteflies had been in the field for three generations and had thus had plenty of time to exhibit any host preference which might exist.

Since there were 576 large plants, many with 30 to 40 leaves, it was obviously impossible to count the third instar larvae and pupae on every leaf of every

plant and a method of sampling had to be elaborated. The best method was found to be removal of the lowest ten leaves of each plant and counting the pupae and third instar larvae on these. As the adult whitefly oviposit on the largest leaves of the seedling plants in the first generation and each successive generation moves up to the next one or two whorls of leaves, the ten lowest leaves present on the plant in September bear practically all the progeny of the second generation. The largest leaves of the plant, on which earlier individuals have been reared, have fallen off by this time.

As will be seen from table 6 the statistical treatment of the data obtained in this experiment gave results which show conclusively that a very marked order of host preference is exhibited by *A. brassicae*.

TABLE 6.

Plant	Mean no. of larvae per square inch of leaf surface	Significance by *t* test
(1) " Extra Curled " scotch kale .	5·01	1>8.7.6.5.4.3. at 0·1% point [1>2. at 5% point]
(2) " Standwell " broccoli . .	4·18	2>8.7.6.5.4. at 0·1% point
(3) " Wroxton " brussels sprouts .	3·66	3>8.7.6.5.4. at 0·1% point
(4) Purple sprouting broccoli . .	1·95	4>8.7.6. at 0·1% point
(5) " Perfection " broccoli . .	1·74	5>8.7.6. at 0·1% point
(6) White sprouting broccoli . .	0·60	—
(7) " Best of All " savoy . .	0·39	—
(8) " Enfield Market " cabbage .	0·03	—

Certain cultivated varieties of *Brassica oleracea* arranged in the order in which they were preferred by *A. brassicae*. The last column in the table showing the statistical significance of this order of arrangement as determined by the *t* test. [Standard error = 28·76% of general mean.]

All varieties were obtained from Messrs. Sutton and Sons, Reading.

6. SENSORY REACTIONS.

The problem of the method by which *A. brassicae* adults discover their host-plants is very difficult, since many biotic and physical factors of the environment may combine to lead the whitefly to its host. Two primary factors have been studied :—

(*a*) The olfactory response of *A. brassicae* to its food-plant or to extracts of the same.

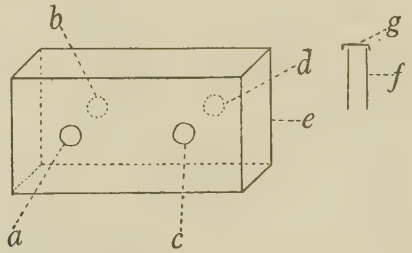
(*b*) The response of *A. brassicae* adults to light of different wave-lengths.

(*a*) It will be noticed from the list of host-plants given that *A. brassicae* apparently chooses its host-plants from the Cruciferae in particular, and it was thought possible that adult whiteflies are attracted to the Cruciferae by an olfactory sense and kept there by a gustatory sense. This idea is supported by the discovery of Verschaffelt (1910) that the leaves and stems of Cruciferous plants contain the strong smelling glucoside sinigrin. Verschaffelt was also able to show that *Pieris rapae* (L.) and *P. brassicae* (L.) exhibit strong chemotropism towards sinigrin and that its presence in the leaves of certain plants determines the selection of the latter as host-plants. In order to test

experimentally whether adult whiteflies exhibit any olfactory response towards the odour of their host-plants an olfactometer of the design described by McIndoo (1926) was constructed. This apparatus failed, however, to throw much light upon the olfactory responses of *A. brassicae*. It was found with this apparatus, however, that the adult insects choose a region of high humidity in preference to one of low humidity, and it is possible that this is one of the major responses of the insect in its natural state.

Since experiments with this apparatus failed to decide whether *A. brassicae* exhibited any chemotropism towards the odour of its host-plant, a different type of apparatus was devised to study this point. This apparatus consisted essentially of a light-tight box two feet long, by one foot high, by one foot broad. On one side of this box were bored two holes of 4·5 inches diameter, and over each of these a cone of fine-mesh wire gauze was tacked. The wire-gauze cones were covered by glass beakers, one of which contained a crushed cabbage leaf between two thicknesses of fine muslin, and the other a pad of wet filter-paper between the thicknesses of muslin. The substance to be tested was wrapped between these folds of muslin in an attempt to eliminate any visual response to the colour of the crushed cabbage leaf. One hundred newly emerged adult male whiteflies and 100 similar females were liberated in the dark box two hours before each experiment, the holes and wire-gauze cones being covered with darkened beakers so that the whole apparatus was light-tight. After two hours the darkened beakers were replaced by the beakers containing the prepared cabbage leaf and filter-paper, and the side of the box containing the holes was turned towards the window. At the end of an hour a count was made of the number of whiteflies caught in each beaker and unable to find their way back into the box, should they wish to do so, on account of the cones. It was found that on the average 77% of the whiteflies caught in the beakers were present in the one containing the crushed cabbage leaf, and the sexes were present in approximately equal numbers. It was concluded from this that *A. brassicae* does exhibit a definite chemotropic response to the odour of its host-plant. Possibly, if a better apparatus be devised, a more definite olfactory response towards the host-plant would be demonstrable.

(*b*) In order to study the response of *Aleurodes brassicae* to light of different wave-lengths the following apparatus was constructed.



5

Fig. 5.—Apparatus for the study of the responses of *A. brassicae* to light of different wave-lengths; *a*, *b*, *c*, *d* = holes to take tubes similar to *f*; *e* = dark chamber, 2′ × 1′ × 1′; *f* = glass tube rendered light-tight with matt black enamel; *g* = filter in spring mount.

In each of the first series of experiments, which were conducted in daylight in the open air in diffuse light, one tube on each side of the dark box was covered

with a colourless filter of optical glass known to allow light from 4000 Å. to 7000 Å. to pass through it, and the other tubes were covered with various filters which were known to transmit light only of a certain wave-length. (The intensity of the light passing through the filters chosen was found to be approximately equal as measured by a photoelectric cell, except in the case of the colourless filter, which was carefully screened until the intensity approximated that of the others.) One hundred newly emerged male whiteflies and 100 similar females were liberated in the dark box in each experiment. At the end of two hours the number and sex of the whiteflies which had collected in each of the four tubes was determined. Within a range of wave-length from 4000 Å. to 7000 Å. the vast majority of the insects had, in response to the light stimulus, collected in the tubes bearing the colourless filters, except where filters of a greenish-yellow colour transmitting light only of a wave-length of 5000–6000 Å. were used. In these latter cases, approximately 76% of the whiteflies, both males and females, which responded, collected in the tubes bearing filters of this colour.

In a further series of experiments, the number of whiteflies collecting in tubes with colour filters transmitting light of different wave-lengths was compared with the number collecting in the tubes bearing filters of the greenish-yellow colour of a wave-length of 5000–6000 Å. In every case the vast majority of whiteflies of both sexes, collected in the latter tubes. It therefore appears that adult *A. brassicae*, of both sexes, respond to light of a wave-length of 5000–6000 Å.

It is noteworthy that Lloyd (1922) found that the greenhouse whitefly, *Trialeurodes vaporariorum* Westw., also responds to light of about this wave-length, which is approximately that of the light reflected from the leaves of its host-plant. It seems probable that the response of whiteflies to this colour is of importance to them in the finding of their host-plant.

7. The effects of the insect on the host.

Only in cases of very young plants or when the infestation is very heavy does *A. brassicae* totally destroy its host-plant, although when present in only moderate numbers it has a pronounced and easily discernible effect. This is probably due to two factors :—

(*a*) The adults and larvae living on the undersurfaces of the leaves freely excrete a sugary " honey-dew " which is shed chiefly on the leaves situated immediately below the one on which they are living. This " honey-dew " helps to block up the stomata of the leaf and hinder the assimilation of the host-plant, and it also proves to be an extremely good medium for the growth of such fungi as *Cladosporium herbarum*, *Alternaria* sp., and occasionally *Capnodium salicinium* and *Meliola* sp., as well as various yeasts. These spread out over the leaf surface hindering assimilation and transpiration and eventually killing the leaf.

(*b*) Both the adult and larval whiteflies pierce the tissues of the host-plant with their stylets and, although there is no evidence that they are the vectors of any virus disease of *brassica*, they certainly must remove a considerable amount of nutritive substances from the plant. To gain knowledge, in the field, of the food substances of *A. brassicae* and hence of the actual damage to the host-plant, would entail quantitative analysis of all the possible nutritive substances used by the insects in the leaf, both before and after infestation. This would be very difficult to effect and would be complicated by fluctuations

in the amounts of substances present in any given leaf during life due to assimilation and translocation. It seemed better to approach the subject by an indirect method and try to find out what food-substances *A. brassicae* could use, and then to construct a series of artificial media containing these substances in different combinations to determine whether *A. brassicae* can live on them or not. From this study some idea of the substances occurring in the host-plant and diminished by the feeding of *A. brassicae* could be obtained.

In order to test the digestive tract of *A. brassicae* for enzymes, the alimentary canal was divided into two regions, the foregut and the mid and hind gut, each of these regions being tested separately. The salivary glands were also tested for enzymes. The methods used were those elaborated by Pickford and Dorris (1934) and Herford (1935).

(1) *Proteolytic ferments.*

The proteolytic enzymes were investigated by means of an unexposed Eastman lantern plate fixed in 2% sodium thiosulphate and well washed and dried in order to remove all traces of silver salts from the gelatine. Individual whiteflies were dissected, the gut and salivary glands being carefully removed and kept moist. In each experiment the foregut, mid and hind gut, and salivary glands of ten individuals were placed in separate groups, and each was pounded up in ten drops of phosphate buffer solution of a definite pH value. Four drops of fluid from each of these regions of the gut and also from the salivary glands, all in buffer solution of the same pH, were placed on the gelatine plate, which was then placed in a desiccator, the walls of which were lined with filter-paper soaked in a buffer solution of the same pH as that at which the tests were being made. On another piece of lantern plate in the same desiccator were drops of pure buffer solution, and drops of buffer mixed with extracts from the different regions of the gut and one drop of neutral 4% formalin which destroyed any enzyme present. In every case these control drops were at

Table 7.

Salivary glands. Per cent. of experiments showing the following degrees of digestion				Foregut. Per cent. of experiments showing the following degrees of digestion				Mid and hind gut. Per cent. of experiments showing the following degrees of digestion				pH of extract	Control		
N.	S.	M.	C.	N.	S.	M.	C.	N.	S.	M.	C.		1	2	3
100	0	0	0	100	0	0	0	100	0	0	0	2	—	—	—
100	0	0	0	100	0	0	0	100	0	0	0	3	—	—	—
100	0	0	0	100	0	0	0	100	0	0	0	4	—	—	—
100	0	0	0	100	0	0	0	100	0	0	0	5	—	—	—
100	0	0	0	100	0	0	0	100	0	0	0	6	—	—	—
100	0	0	0	10	90	0	0	0	100	0	0	7	—	—	—
100	0	0	0	10	0	70	20	10	0	0	90	8	—	—	—
100	0	0	0	90	10	0	0	0	30	30	40	9	—	—	—
100	0	0	0	100	0	0	0	100	0	0	0	10	—	—	—

N = No digestion.
S = Slight digestion.
M = Moderate digestion.
C = Complete digestion.

1 = Salivary glands.
2 = Foregut.
3 = Mid and hind gut.

The results of experiments conducted to determine whether *A. brassicae* has a proteolytic ferment capable of breaking down gelatine. 50 experiments were conducted in all.

the same pH and concentration of extract as the experimental drops. The desiccators were kept at a constant temperature of 20° C. for twelve hours, to incubate the extracts and allow digestion to take place. At the end of this time the plates were removed and rapidly immersed in 4% formalin to stop all enzyme action. They were then washed and stained for three hours, acid fuchsin being used for the extracts of acid pH, and Delafield's haematoxylin for those of an alkaline pH. If digestion of the gelatine was complete a clear ring appeared on the stained plate where the drop had been, and a lighter ring appeared when only partial digestion had occurred. The results of these experiments to determine whether adult female *A. brassicae* possess any proteolytic ferments are tabulated below.

From the above table it will be seen that adult *A. brassicae* have, mainly in the region of the mid and hind gut, an enzyme capable of digesting gelatine. At 20° C. this enzyme is most active within the pH range 7 to 9, whereas no digestion at all took place in any of the controls. It is probably a fair assumption that this enzyme is tryptic, although so far no experiments have been undertaken to decide this point.

(2) *Amylase.*

In order to determine whether *A. brassicae* adults possess a starch-splitting enzyme the technique elaborated by Pickford and Dorris (1934) was first employed, and later that used by Herford (1935) in his study of the secretion of diastase by the Jassid, *Empoasca solana* DeLong. In the first method a hot 2% solution of starch was mixed in equal proportions with a hot 2% solution of agar-agar and the mixture was poured quickly over a clean, previously heated, glass plate, which was immediately drained, first to one side and then to the other, in order to obtain a thin even film. When these plates were thoroughly dry, tests were made on them in a similar manner to those for proteolytic ferments except that N/10 iodine was used for three minutes for staining. The results obtained are shown in the table below.

Table 8.

Salivary glands. Per cent. of experiments showing the following degrees of digestion				Foregut. Per cent. of experiments showing the following degrees of digestion				Mid and hind gut. Per cent. of experiments showing the following degrees of digestion				pH of extract	Control		
N.	S.	M.	C.	N.	S.	M.	C.	N.	S.	M.	C.		1	2	3
100	0	0	0	100	0	0	0	100	0	0	0	3	—	—	—
100	0	0	0	100	0	0	0	100	0	0	0	4	—	—	—
60	40	0	0	70	30	0	0	100	0	0	0	5	—	—	—
10	10	60	20	20	0	70	10	80	20	0	0	6	—	—	—
0	0	0	100	0	0	0	100	0	40	60	0	7	—	—	—
0	0	0	100	0	30	10	60	80	20	0	0	8	—	—	—
10	60	20	10	70	30	0	0	100	0	0	0	9	—	—	—
90	10	0	0	100	0	0	0	100	0	0	0	10	—	—	—

N = No digestion.
S = Slight digestion.
M = Moderate digestion.
C = Complete digestion.

1 = Salivary glands.
2 = Foregut.
3 = Mid and hind gut.

The results of experiments conducted to determine whether *A. brassicae* has a starch-splitting enzyme. 50 experiments were conducted in all.

From this table it appears that *A. brassicae* has, mainly in its salivary glands and foregut, a starch-splitting enzyme working between pH 6 and 9.

It will be observed that both in the case of the proteolytic and the starch-splitting ferments the indications of the presence of the enzyme are not completely restricted to any particular portion of the alimentary canal. An attempt to determine the pH of the separate regions of the gut was not very successful, probably owing to their small size, but the average pH of the whole alimentary canal of 50 specimens was about 7, and some evidence was obtained indicating that the mid and hind gut is slightly more alkaline than the foregut.

In the method elaborated by Herford (1935), a solution of 5% starch and 1% agar was made up and 5 cubic centimetres were placed in each of 100 specimen tubes one inch in diameter. When cool, three drops of a solution of paraffin wax in ether was placed on the surface of the starch–agar, so as to form an exceedingly thin wax membrane. (The presence of some sort of membrane was found to be essential to induce the insects to feed.) The tubes were then plugged with cotton-wool and autoclaved for one hour. Fifty of these tubes had 25 newly emerged whiteflies liberated in each, the tubes being suspended upside down. The insects could be seen feeding normally through the wax membrane, and some oviposition occurred. At the end of five days the insects were removed, the wax removed by treating with ether and the starch–agar boiled for five minutes with five cubic centimetres of Fehling's solution, and allowed to cool slowly. In 42 of the tubes in which the insects had been feeding a heavy red-copper precipitate was thrown down, and in five tubes a slight red precipitate was apparent, and in three tubes no precipitate could be found, presumably because the wax membrane was too thick to allow the insects to feed properly. None of the fifty control tubes showed any precipitate on boiling with Fehling's solution. It therefore appears that *A. brassicae* adults secrete an amylase capable of breaking down starch to maltose.

Carter and Cotner (1929) succeeded in isolating certain yeast forms from sugar solutions on which the Jassid, *Eutettix tenellus* Baker, had been feeding; and Herford (1935) described the isolation of a yeast, having the power to secrete diastase, from the alimentary canal of the Jassid, *Empoasca solana* DeLong. Using the technique employed by Herford, attempts were made to determine whether *A. brassicae* possesses a yeast in its alimentary canal. Traces of a yeast were found in the foregut. It is possible, therefore, that the amylase reaction described is due to the presence of a yeast and is not an indication of amylase secretion in the foregut of the whitefly itself.

(3) *Invertase.*

In order to determine whether *A. brassicae* possesses an invertase, tubes were made up containing 5 cubic centimetres of 2% agar and 5% sucrose. Since autoclaving tends to cause inversion of sucrose, both the agar and the sucrose were thoroughly washed in absolute alcohol, dissolved separately in autoclaved distilled water, and mixed while warm. Little or no bacterial or fungal contamination occurred in 100 tubes, all doubtful tubes being neglected. A wax membrane was placed on top of the agar as before. It was found that boiling the sucrose solution for 20 minutes only caused an inversion of 0·7, which proved to be insufficient to cause an observable reduction of Striegler's modification of Fehling's solution. Fifty of the tubes had 25 adults placed in each. At the end of five days the whiteflies were removed, the wax membrane dissolved away with ether, and the sucrose–agar tested for the presence of

reducing sugars. Forty-one of the tubes that had contained the experimental insects gave a heavy red-copper precipitate after boiling with Fehling's, one tube showed no reduction, and the remaining eight tubes were discarded owing to traces of fungal contamination. None of the control tubes gave a positive result when tested for reducing sugars. It therefore appears that adult *A. brassicae* secrete an invertase which is capable of inverting pure sucrose, and which is ejected into the tissues of the food plant with amylase when the insect is feeding.

(4) *Culture on artificial media.*

An attempt was next made to induce *A. brassicae* adults to live and, if possible, to breed on the six following artificial media :—

(1) 0·05% Methylene blue + 5% sucrose + 2% agar-agar.
(2) 0·05% Methylene blue + 5% sucrose + 2% starch + 2% agar-agar.
(3) 2% starch + 2% agar-agar.
(4) 0·05% Methylene blue + 5% sucrose.
(5) 0·05% Methylene blue + 5% sucrose + 2% starch.
(6) 2% starch solution.

As controls 2% agar-agar was used for the agar cultures and distilled water for the liquid cultures. No attempt was made to provide any accessory food substances. Methylene blue was added to the media so that it was possible to see from the coloration of the dissected gut of an insect whether the medium had been taken up or not. It was found necessary to use some form of membrane in each case, since experiments showed that *A. brassicae* will not feed unless it first has a membrane to pierce. Various membranes were tested (collodion, cellophane and cod's swim bladder), but by far the most satisfactory was found to be pig's bladder preserved in equal parts of pure glycerine and

TABLE 9.

Medium	Mean length of life of adult in days	Mean no. of eggs laid per ♀	No. of 1st instar larvae produced per ♀	Mean length of life of 1st instar larvae in days	Mean length of life of adult on control medium in days	Mean no. of eggs laid per ♀ on control medium
0·05% Methylene blue + 5% sucrose solution + 2% agar	12	0·08	0	0	3·2 (agar)	0
0·05% Methylene blue + 5% sucrose solution + 2% starch sol. + 2% agar	14·8	0·28	0·1	3	3·4 agar)	0
2% starch solution + 2% agar	8·4	0	0	0	2·6 (agar)	0
0·05% Methylene blue + 5% sucrose solution	10·3	1·2	0·2	2	2·6 (water)	0
0·05% Methylene blue + 5% sucrose solution + 2% starch sol.	12·8	0·92	0·2	3	4·2 (water)	0
2% starch sol.	6·9	0	0	0	2·5 (water)	0

The results of experiments on the length of life and reproductive powers of *A. brassicae* on various artificial media. 50 whiteflies used in each experiment and in controls.

4% formalin, and scraped down to the thinnest possible layer and thoroughly washed under running water before use. The media were placed in small lipped watch-glasses, a membrane stretched tightly over each, and the whole was inverted over the mouth of a gauze cage containing newly emerged adult whiteflies. Experiments on 50 individuals were conducted with each medium. The results of attempts to keep *A. brassicae* on these media are given in table 9.

From these experiments it was concluded that adult *A. brassicae* are able to live for some time on solutions containing sugar, to a less degree on starch solutions, and best of all on sucrose and starch mixed, although no very definite conclusions can be drawn, probably owing to imperfections in technique. However, considering that *A. brassicae* has a powerful amylase capable of breaking down starch to sugar, and that it can live for some time on solutions of starch and sucrose, it appears probable that the whiteflies live on these in nature and damage the host-plant by removal of these and other nutritive substances from its tissues.

8. Summary.

(*a*) The egg and larval instars of *A. brassicae* are described and figured.

(*b*) Four or five generations per annum were observed at Cambridge between May and October. Slightly more females than males are present in the field at this time. During the winter males that have paired die, but the females pass the winter in sheltered places on the host-plants and can withstand a temperature of −14° C.

(*c*) The sex ratio of adults obtained from fertilised eggs was found to be ♂♂ : ♀♀ = 1 : 1·04. The sex ratio of individuals derived from parthenogenetic eggs was ♂♂ : ♀♀ = 1 : 0·09. In other words, parthenogenetic eggs practically all give rise to males, whereas eggs from impregnated females give rise to approximately equal numbers of males and females.

(*d*) Host selection was studied in some detail, and twenty-three varieties of plants were tested. Large-scale experiments, conducted both in the laboratory and in the field, to determine whether *A. brassicae* adults show any host preference are described. The results show that whiteflies exhibit very marked preference for certain varieties of *Brassica oleracea*.

(*e*) A well-marked olfactory response of *A. brassicae* to the odour of its host-plant was observed and experiments in this connection are described.

The response of the insect to light of different wave-lengths was found to be greatest between 5000–6000 Å. This wave-length approximates to that of the light reflected from the leaves of its host-plants.

A. brassicae adults tend to move from a region of low relative humidity to one of high humidity.

(*f*) The insect is capable of living up to fifteen days on artificial media containing starch and sugar, and for a shorter period when starch or sugar alone is present.

(*g*) Tests indicate that a proteolytic enzyme occurs in the mid and hind gut; and amylase in the salivary glands and foregut, while an invertase is also present.

(*h*) It is concluded that *A. brassicae* damages its host-plant by the removal of certain nutritive substances, principally starch and sugars; also by hindering assimilation and transpiration with the wax and honey-dew secreted, the latter also tending to cause further damage by encouraging the growth of certain moulds.

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